

## THE RELATION OF *PIERIS VIRGINIENSIS* EDW. TO *PIERIS NAPI* L.

### SPECIES FORMATION IN *PIERIS*?

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IN A PREVIOUS PAPER (Hovanitz, 1962), it was indicated that a fuller discussion of the relationship of *Pieris napi* L. to *Pieris virginiensis* Edw. would be forthcoming. In that paper, the map showing the distribution of *P. napi* included the distribution of *P. virginiensis* but a closer distinction between the two was not indicated because of the reduced size of the map included. A more detailed map showing the relationships between the two biological entities under discussion is included with this paper, together with a description of the known facts of the lines of separation of the two "species" or races, and a summary of the events that have most probably occurred in relation to the two groups up to the present time.

On the map in the previous paper (Hovanitz 1962), the range of *Pieris napi* L. for the eastern United States included *virginiensis* as well as *napi* itself. The race of *napi* with which we are concerned here is known as *oleracea*. This race blends northwards and westwards into other races by imperceptible gradations. *Pieris napi oleracea* (known also by the summer brood names, *aestiva* Edw., *hyemalis* Edw. and *acadica* Edw.) may be considered the name for the race of *napi* east of 90° Longitude and south of 50° N. latitude, more or less, with the exception of the area south of New York state (38° N). Other names can be found in McHenry (1962). The area south of New York state and east of 90° Longitude is occupied by the race or species *virginiensis*. In New York state and other points in the vicinity, or close to the southern limits of *oleracea*, there are populations which in some cases appear to be more closely related to *virginiensis* than to *oleracea*, and in other cases, are more closely related to *oleracea* with occasional individuals similar to *virginiensis*. The status of the line of contact between *oleracea* and *virginiensis* is not one of free and even blending such as might be expected of freely interbreeding individuals in a case of solely geographical isolation. Populations are rather clearly either *oleracea* or *virginiensis* as the case may be, with only occasional examples of intermediates giving some hint of the nature of introgression at the line of contact.

The contact of these two species or races bears a close relationship to the similar situation between the species or races *Basilarchia astyanax* and *B. arthemis* in the same general area (Hovanitz 1949).

Specimens of *P. napi* studied in various collections have permitted a map to be drawn showing the detailed distribution of *oleracea* and *virginiensis* (fig. 1). On this map, locations where *oleracea* (or *napi* in the species sense) are known are shown by the letter *N* and *virginiensis* locations are shown by the letter *V*. In addition to the indications on the map, there are reasons for assuming that each of these races overlaps the other even greater than seems indicated on the map. Due to lack of specific data (e.g. "New York"), some of these indications could not be shown on the map. These details will be mentioned below.

On the map, it can be seen that *oleracea* extends southwards in the mountains of New England to Connecticut where it comes in contact with *virginiensis* or something like *virginiensis*. It is doubtful that these specimens are truly *virginiensis*, though they do bear some resemblance to them. Instead they are more likely aberrant *oleracea*, which are genetically tending in the direction of *virginiensis* through introgression. In addition, the habitat change out of the Canadian forest typical of *oleracea* to the "Transition" lowlands might lead to a phenotypic alteration in facies. Populations of considerable size are definitely known at the present time in Vermont and New Hampshire. They are not now known in the vicinity of Boston, Mass. though they were common there before 1850. The following bears witness to a reduction in distribution of *napi* in the 1800's:

From Scudder (1889):

"This butterfly is a member of the Canadian fauna . . ."

"It is found throughout New England although seldom abundant south of the annual isotherm of 48°. Northward and eastward it is everywhere abundant and it continues to be so as far south as Williamstown, Mass. (Scudder), Dublin, N. H. (Leonard) and Portland, Me. (Scudder, Verrill). South of 42° N. L. or the northern boundary of Connecticut, it rarely occurs, although it has been taken at Farmington, Conn. (Norton), Newport, R. I. (Miss Coggeshall teste Higginson) and Fire Island Beach, Long Island (Smith). Even in the north, however, there seems to be some local causes for its abundance."

"Mr. Lintner, writing in 1864, says that in Schoharie, N.Y., 'it was extremely rare until recently,' and previous to 1857, 'he had taken it but once in three years . . .'" "Mr. Bacon of Natick, Mass. says that the insect by no means disturbs cabbages and turnips as it did fifteen or twenty years ago."

"I recollect once seeing the college yard in Cambridge, I think it was about 1857, fairly swarming with *P. oleracea*. It is now never found, to my knowledge, anywhere in the region about Boston, and I think it is wholly confined to the less cultivated and especially the hilly districts of New England."

From Klots (1951):

"*Napi* has . . . suffered a great restriction in habitat, and probably in habits, for it is now almost entirely limited to shaded Canadian Zone forest . . .". "Not recorded south of the Catskill Mountains in New York".

From Klots (1935) of Edwards,

"He mentions a female taken by Mead in the last week of June at Stony Clove in the Catskill Mountains . . . many eggs were obtained . . . from the chrysalis an *oleracea* emerged." "Stony Clove is in excellent territory for *napi* (*oleracea*) but I know of no records of *virginiensis* from there." "I have . . . seen specimens of *virginiensis* from Big Indian Valley in the Catskills, where the environment is more suited to *virginiensis*."

"In 1931, near McLean, Tompkins County, New York, I was able to obtain undoubtedly authentic eggs, larvae and chrysalis of *virginiensis*, through watching females ovipositing on *Dentaria diphylla* Michx."

From Fiske (1901):

"*Pieris napi*, once common enough to be injurious to cabbages and other cruciferous plants throughout New England, has since the introduction of *rapae* become one of our rarest butterflies. Its range is now restricted to the northern and mountainous portions, and even in the fortresses of the White Mountains it is a scarce insect."

The eighteenth century idea of a "species" contributed a lot to a general confusion of the nature of the relationship between *oleracea* and *virginiensis*. It was then, and too often now, the general idea that a species was represented by a specific morphological type, without regard to the variation which a population may have within itself. Some of the best collectors and breeders of Lepidoptera have therefore become confused, having the all pervading desire to designate some biological unit as either a "species", subspecies or variety when the true relationship may not be possible with only these tools of nomenclature. For example, Edwards (1881) says:

"*Virginiensis* . . . has become a true species, although unquestionably, in a higher latitude, it appears as an occasional aberration only of *Oleracea*."

Also, Klots (1951) says:

"Until very recently, *virginiensis* has been confused with *napi*, but it is now known to be a distinct species of more southern (Transition Zone) distribution."

Edwards (1868-1872) says:

"In the Kanawha district, it replaces *Oleracea* which is yet unknown there. It is not uncommon in the month of May, frequenting open woods rather than gardens, and in this respect differing in habit from the allied species. I have never met with it later than June, though *Oleracea*, in the Northern States is most abundant after that month and continues breeding till the early autumn frosts." "I have received specimens of *Virginiensis* from Mr. Wm. Saunders of London, Canada and am informed by him that it is there a rare insect."

#### DIFFERENCES BETWEEN *P. NAPI OLERACEA* AND *P. NAPI VIRGINIENSIS*

The primary visible differences between *P. napi oleracea* and *P. napi virginiensis* can be observed in figs. 2 and 3. In figure 2 is shown the male and female of the upper side of *virginiensis* to the left; at the same location in figure 3 is shown the under side. These specimens are

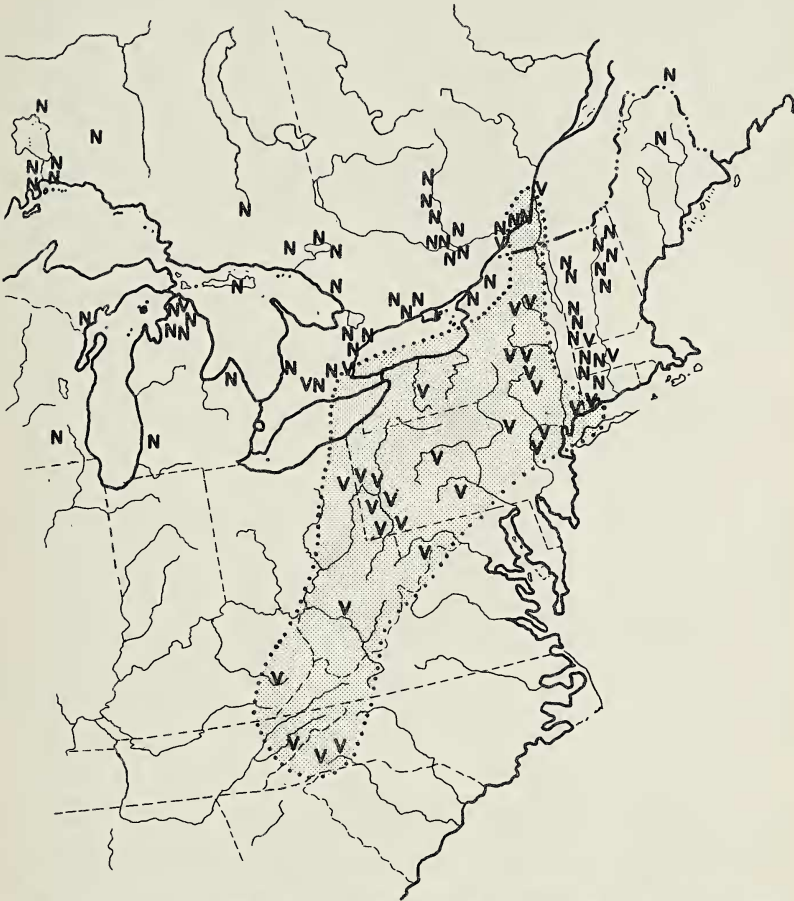


Fig. 1. Map showing the distribution in the eastern part of North America of the introgression area of *Pieris napi* races *virginiensis* and *oleracea*.

from near Pittsburgh, which although toward the north end of the range of *virginiensis* are quite typical of the populations south through the Appalachian mountains. The pattern of the upper side female should be noted as quite typical of this race, and which is only rarely present in *oleracea*. Of critical distinction, the pattern of the under side of the wings should be noted. The veins are outlined in a tan pigmentation, not heavy but rather broad in expanse, in appearance unlike any other race of *napi*.

*P. napi oleracea* is shown in figures 2 and 3 by the central two specimens; these are from southern New Hampshire which is near the



Fig. 2. LEFT: *P. napi virginensis*, TOP: male, BOTTOM: female. Both Powdermill Nat. Res. nr. Rector, Westmoreland C. Pennsylvania April 26, 1958. Clench.  
 CENTER: *P. napi oleracea*, TOP: male, BOTTOM: female. Both Jefferson, N. H. May 13, 1932. P. J. Lennox.  
 RIGHT: *P. napi oleracea*, TOP: male, Lincoln, Maine, July 14, 1935. BOTTOM: female, Jefferson, N. H. May 13, 1932. P. J. Lennox.

*all upper side facies*



FIG. 3. Same as fig. 1, but all lower side facies

southern part of the distributional range of this species. They are however typical in appearance. Note the difference between the two races on both the upper and lower surfaces: *virginiensis* is more of chalky white on the upper side as compared with *oleracea*; the wings on the upper side tend to be veined with black near the borders and cell in *oleracea* which is replaced with a brownish "rapae-type" pattern in *virginiensis*; on the under side the veins are heavily lined with black in *oleracea* in a way distinctive from that of *virginiensis*; and there is a yellowish suffusion on the under side of the wings in *oleracea* not present in *virginiensis*. On the other hand, the appearance of *oleracea* changes during the seasons while that of *virginiensis* does not. There is no indication that *virginiensis* has more than the one generation per year, this occurring in early May whereas *oleracea* has a succession of generations starting in April and extending throughout the year until the cold weather of the autumn. During this extended period the weather conditions are quite different, and the effects of this on the appearance of *oleracea* are profound. The appearance of the adults emerged during the warmer part of the season are quite different. A specimen of the summer brood is shown in figures 2 and 3 at the upper right. Note the slightly increased size but more important the almost complete absence of any pigment other than white on the wing surfaces. These summer forms have been given the names *hyemalis*, *acadica* and *aestiva* by Edwards for the general area under consideration. As a racial name, the only one of any significance however is *oleracea*. Throughout the ranges of these races, there is fairly good uniformity in pattern and characteristics; however, it should be pointed out that within each of these races and especially *oleracea* there is a great amount of variation which tends to blend the two together. For example, a specimen at the bottom right in figures 2 and 3 is from a population of *oleracea* but shows the "rapae-type" pattern of *virginiensis*. The underside of the wings however makes clear that the specimen is *oleracea*.

Areas of typical *oleracea* may be described as follows: The Canadian forest areas ranging from northern Michigan across northern Ontario and Quebec into eastern Quebec, New Brunswick, Nova Scotia, Maine and the mountainous parts of the New England states as far as Massachusetts. South of these points and until the typical populations of *virginiensis* are reached in New York state, Ohio and Pennsylvania, the populations apparently are in a state of uncertainty regarding a complete divergence from the *virginiensis* or the *oleracea* genome and all the things pertaining thereto, including in addition to pattern differences, the physiological alterations required for the more southern existence, the univoltine life cycle and the changed food plant preferences. These intermediate populations lie in a line ranging from Michigan, across southern Ontario to Montreal in Quebec and southward to the Catskill Mountains of New York. Some of these can be distinguished as *oleracea* with *virginiensis* tendencies and others as *virginiensis* with *oleracea* tendencies, though the former outrank the latter. Populations which

would be considered *oleracea* with *virginiensis* tendencies would be the following, with an indication of the extent of the tendency:

Michigan: Emmett Co., north part of southern peninsula (slight)  
 Ontario: region around London, Huntsville, Sydney Field station,  
 Marmora, Trenton (considerable)  
 ———: Aylmer, Bells Corners, Britannia, South March, Merivale,  
 Constance Bay, Ottawa West (slight)

Quebec: Harrington Lake, Gatineau Park (slight)

Massachusetts: Cummington, Whately, Franklin Co., Mt. Greylock  
 Populations which would be considered *virginiensis* with *oleracea*

tendencies would be:

Quebec: Ile Perrot (Montreal)

New York: the Adirondacks, the Catskills, Ilion, McLean

Ontario: Hamilton

Populations with little sign of intergradation on the northern end  
 of the range of *virginiensis*:

Pennsylvania: Scranton, New Brighton, Pittsburgh, Forbes Forest,  
 Charlevoix, Showville, Washington Co., Fayette Co., Lawrence Co.

Ohio: Canton

West Virginia: Forks of the Kanawha, Coalburgh

#### HABITS OF THE RACES

The rather distinct break between the geographical ranges of *oleracea* and *virginiensis* would seem to need some isolation barrier for the maintenance of its integrity. This barrier is clearly not one of water or mountain but rather one of habitat selection and the accompanying biological changes in the physiology of the races concerned. For some idea of the field habits of these races, we may refer to other authors:

Klots (1951) says of *virginiensis*:

"Until very recently, *virginiensis* has been confused with *napi*, but it is now known to be a distinct species of more southern (Transition Zone) distribution. Its dark markings are a more smoky, diffuse brown and it lacks the yellowish tint beneath, on the HW and apex of the FW, which *napi* usually has. It is single brooded. More even than *napi*, it is limited to woods and very local."

"Food: — Toothwort (*Dentaria diphylla*), probably other *Dentaria*. One brood. Adults in early May (central New York)."

"Range:—Transition Zone, Ontario, central New England and New York, s. to Virginia (TL. Kanawha, West Virginia)."

He says of *napi oleracea*:

"*Napi* has . . . suffered a great restriction in habitat, and probably in habits, for it is now almost entirely limited to shaded Canadian Zone forest . . . *P. virginiensis* lacks yellowish beneath on the HW and apex of the FW and has the scaling along the veins of the HW and costa and apex of FW beneath much more diffuse and powdery looking. A rare dark form of *P. rapae* lacks dark spots above, but never has the dark-lined veins of *napi*, and has heavier scaled, less fragile looking wings."

Food. Formerly, at least, nearly any cultivated or wild cruciferae; now probably chiefly limited to native, woodland species, such as toothworts (*Dentaria*), Rock cresses (*Arabis*), Winter and Water cresses (*Barbarea*), etc.



Three broods. Adults in late April (Massachusetts)." "Not recorded s. of the Catskill Mountains in New York."

Clark (1951) says of *virginiensis*:

"Range:—One record, Frederick County northwest of Cross Junction on the Bloomery Road (Rank 698) about 200 feet east of the West Virginia line, April 24, 1938."

"Variation — This species varies considerably in the intensity of the bordering of the veins on the under side of the hind wings. This bordering is pale in all the individuals from Virginia and adjacent West Virginia that we have seen, some having the under side of the hind wings almost immaculate white."

"Occurrence:—Confined to rich deciduous woods and extremely local, occurring in limited numbers at usually widely separated localities. The reduction in the numbers of *Pieris virginiensis* and its present occurrence only in widely separated localities are undoubtedly the result of deforestation, which has greatly reduced the areas in which it is possible for it to maintain itself." "*Pieris virginiensis* keeps strictly to the woods."

"Season:—One brood. This species appears shortly after the middle of April and flies until about the middle of May."

Clench (1958) writes of the same:

"*Pieris virginiensis* . . . common in woods . . . one brood: Late April to mid-May. One . . . capture . . . on 4 June, 1958 is surely a freak occurrence . . ."

Scudder (1889) writes of the habits of *oleracea*:

"Food plants. This caterpillar feeds on various cultivated cruciferous plants, such as turnip (*Brassica rapa*), cabbage (*B. oleracea*), radish (*Raphanus sativa*), horseradish (*Nasturtium armoracia*) and mustard (*Sinapis*). Mr. Lintner considers that it prefers turnip to cabbage, for he once obtained fifty eggs from a turnip bed and could find none on adjacent cabbage plants of the same age, and this has been my experience." Hoy, on the other hand, thinks it is found mostly on mustard. But it also occurs on some of our native plants, such as *Arabis drummondi* (Couper) and *A. perfoliata* (Fletcher), and Fitch says it occurs abundantly on the water cress (*Barbarea vulgaris*)."

"Life History. This butterfly, which appears to be generally triple brooded, passes the winter in the chrysalis, the first brood has been seen as early as April 18, but usually appears between April 27 and May 9, a week or thereabouts after *P. rapae*. For several years Fitch observed it at East Greenwich, N. Y. for the first time on May 8 and 9 and only once as early as May 6; in northern localities it is sometimes as late as the third week in May. It usually becomes abundant between the 10th and 15th of the month and continues until the end of the first week in June. The eggs are laid during the last half of May and early in June, and hatch in from 5 to 10 days . . . the second brood . . . makes its advent during the last days of June or early July . . ., this brood in *oleracea* seems never to be very abundant . . . and to maintain itself for a comparatively short time; it becomes common by the end of the first week in July and sometimes disappears . . . before the end of the month . . . "The third brood appears as early as the last days of July but usually not before August; it . . . lasts until early September . . . Occasional specimens, . . . disclose butterflies late in September or early in October." "The species must be triple brooded in the north."

Edwards (1868-1872) writes of *virginiensis*:

"In the Kanawha district it replaces *Oleracea* which is yet unknown there. It is not uncommon in the month of May, frequenting open woods rather than gardens, and in this respect differing in habit from the allied species. I have never met with it later than June, though *Oleracea* in the

Northern states is most abundant after that month and continues breeding til the early autumn frosts." "I have received specimens of *Virginiensis* from Mr. Wm. Saunders of London, Canada and am informed by him that it is there a rare insect."

These data would tend to confirm the evidence derived from the data of museum specimens that *oleracea* is indeed a multivoltine race which breeds from April all through the year until the Autumn frosts. Our own personal experience on *napi* in California does not conflict with this opinion. Here *napi* (*venosa* and *castoria*) are continuously brooded when possible in relation to temperature and moisture conditions. They go into diapause when conditions of the food plant are unfavorable; this is usually in the summer when the food plant (*Dentaria*) dries up. In fact much of the first winter generation does likewise as *Dentaria* does not stay green long. This accounts for the summer or late spring generations being less abundant than the winter or early spring generations. A similar observation has been made of the generations of *napi* in New England.

The food plant difference between the races *oleracea* and *virginiensis* is important in only one way, namely in the restriction of habitat of *napi* to a different ecological niche. *Dentaria* is a plant of the open woods and partial shade. The flight period of *virginiensis* must be adjusted to meet the proper conditions of moisture requirement for the plant as well as for the degree of light availability in the deciduous forest where early spring may allow more light in the forest than in summer. The restriction of *virginiensis* to the "Transition" life zone forest may be correlated with this light and temperature relationship. The northern forest is cooler all summer long and the temperature needs of *oleracea* can be met usually in the open areas as well as in the partial shade of the forest. This would account for the different flight habits of the two races. In California, *napi* (*venosa* and *castoria*) fly only in the cool canyons where there is partial shade even though there is abundant food available for them outside in the form of wild mustards. Instead they are restricted to *Dentaria* of the shaded woods, while *Pieris rapae* and *P. protodice* fly only a few yards away in the direct sunlight and feed upon mustards.

The food plant of *oleracea* so often indicated in the literature is winter or water cress (*Barbarea*) which is apparently restricted to the vicinity of streams. There is indication that in the Catskill Mountains (New York) there may be a population of *virginiensis* on *Dentaria* while sympatrically there are populations of *oleracea* on *Barbarea*. If this is so, an excellent study could be developed to show the nature of the racial or specific isolation of these two at a region where both maintain reasonably distinct populations in close contact. The fact that *oleracea* flies in April, *virginiensis* in May and *oleracea* again in June and July indicates another additive isolation factor which would help to maintain the species or racial distinctness.

By way of conclusion, the data presented show rather conclusively that *Pieris napi oleracea* and *Pieris napi virginiensis* are not as com-

pletely separated as one might wish "species" to be but that they are not either fully racial or subspecific in the sense that their populations blend into one another as by a continual gene flow. It is therefore a matter of personal opinion whether they should be considered species or races for nomenclatorial purposes. For these purposes it is impossible to stand on the middle ground as a choice must be made. I choose to use the racial designation for the reason that the groups are almost completely allopatric, that is, the populations are geographically separated and do not occur in the same place with certainty without interbreeding and complete fusion. Also, intermediates do occur with high frequency in intermediate geographical areas. There is work to be done in this regard on the ground in important areas, such as, the Catskill Mountains, Ile Perrot (Montreal) or any other areas where a potential close unity of the two appears.

The past changes in the distribution of the species have been greatly exaggerated, especially with regard to any competition between *P. rapae* and *P. napi*. The habits of the two species are so distinct that no competition can reasonably exist. Past records of *P. napi* feeding on garden or cultivated cruciferous plants are undoubtedly correct but these larvae came from adults flying out of adjacent woods to lay their eggs on any cruciferous plants available. With the destruction of the woods in the New England states, the habitat for *napi* disappeared and then of necessity *napi* disappeared. This was the situation for the low lands. In the mountains, *napi* still exists as it did in the past.

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